

A new Pacific Ocean species of *Typhlonida* Macpherson & Baba, 2022 (Crustacea, Decapoda, Munididae) from the flank of the emergent seamount Isla del Coco (Costa Rica) with notes on the phylogeny of the genus

Dong Dong¹, Charlotte A. Seid², Xinzheng Li^{1,3,4}, Greg W. Rouse²

1 Department of Marine Organism Taxonomy & Phylogeny, Qingdao Key Laboratory of Marine Biodiversity and Conservation, Institute of Oceanology, Chinese Academy of Sciences, Qingdao 266071, China

2 Scripps Institution of Oceanography, University of California San Diego, La Jolla, CA 92093, USA

3 University of Chinese Academy of Sciences, Beijing, China

4 Laoshan Lab, Qingdao 266237, China

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Corresponding authors: Greg W. Rouse (grouse@ucsd.edu); Xinzheng Li (lixzh@qdio.ac.cn)

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Abstract

The genus *Typhlonida* Macpherson & Baba in Machordom et al. 2022 is a group of munidid squat lobsters typically found in deep waters. This study describes and illustrates a new species, *Typhlonida cocoensis* **sp. nov.**, from a seamount area in the eastern Pacific. *Typhlonida cocoensis* **sp. nov.** is closely related to *T. sanctipauli* (Henderson, 1885) but can be readily distinguished from the latter by its relatively small eyes, narrow anterior margin of the thoracic sternite 4, lack of granules on the lateral surfaces of sternite 7, and unarmed anterior branchial regions dorsally. In addition to morphological comparisons, genetic distance and phylogenetic analyses were used to support the recognition of this new species. The phylogenetic positions of the *Typhlonida* and *Antillimunida* species from the eastern Pacific are discussed.

Key Words

Eastern Pacific, phylogeny, squat lobsters, taxonomy, *Typhlonida*

Introduction

Munididae is a family of squat lobsters typically living in the deep waters of the continental shelf and slope (Baba et al. 2008). It is one of the most diverse groups of marine invertebrates in the world, currently containing 497 species worldwide (Machordom et al. 2022). *Munida* Leach, 1820, was once the largest genus in the Munididae, until it was divided into 11 genera by Machordom et al. (2022) based on morphological, molecular, and biogeographic analyses. Species with minor morphological differences have been shown to have significant genetic divergence (e.g., Macpherson et al. 2024). Given the complex interspecific

variation and morphological similarity among some of these genera, molecular analysis is becoming necessary in the taxonomic determination of munidid species.

Despite the high species richness around the world, munidids show remarkably low biodiversity in the eastern Pacific, i.e., off the Pacific coast of the American continents. Only 22 species in seven genera have so far been reported from this vast area (Hendrickx 2003; Baba et al. 2008; Hendrickx and Ayón-Parente 2010; Liu et al. 2020; Gallardo Salamanca et al. 2021; Machordom et al. 2022): *Antillimunida bapensis* (Hendrickx, 2000), *A. gracilipes* (Faxon, 1893), *A. hispida* (Benedict, 1902), *Babamunida obesa* (Faxon, 1893), *Dactylonida mexicana* (Benedict,

1902), *Grimothea curvipes* (Benedict, 1902), *G. debilis* (Benedict, 1902), *G. gregaria* (Fabricius, 1793), *G. johni* (Porter, 1903), *G. lipkeholthuisi* (Hendrickx & Ayón-Pariente, 2010), *G. macrobrachia* (Hendrickx, 2003), *G. monodon* (H. Milne Edwards, 1837), *G. montemaris* (Bahamonde & López, 1962), *G. planipes* (Stimpson, 1860), *G. quadrispina* (Benedict, 1902), *Iridonida refulgens* (Faxon, 1893), *I. tenella* (Benedict, 1902), *I. williamsi* (Hendrickx, 2000), *Trapezionida diritas* (Gallardo Salamanca & Macpherson, 2021), *Typhlonida perlata* (Benedict, 1902), *T. propinqua* (Faxon, 1893), *T. alba* (Liu, Li & Lin, 2020). *Typhlonida microphthalma* (A. Milne-Edwards, 1880) was once reported from Cocos Island (Faxon, 1893, 1895), but the record was questionable (Hendrickx 2000; Baba et al. 2008).

Unlike in other regions, some species of Munididae in the eastern Pacific, such as *G. monodon* and *G. johni*, can aggregate into large populations and are therefore of high commercial value, so the genetic diversity and evolutionary history of those species are well documented (e.g., Haye et al. 2010). In contrast, most species are still seldom reported due to their restricted distribution, deep-sea habitat, or low abundance, and therefore remain poorly studied at the genetic level (Hendrickx 2000, 2021). Genetic data are available for only nine species in the eastern Pacific for phylogenetic studies.

In January 2019, a research expedition was organized to investigate the biodiversity of deep-sea seamounts off the Pacific margin of Costa Rica, during which several munidid specimens were collected. A new species of *Typhlonida* Macpherson & Baba in Machordom et al. 2022 was recognized after morphological examination and molecular analyses. The phylogenetic relationships of species within the genus *Typhlonida* were investigated through a phylogenetic reconstruction including the new species and other newly sequenced species from the eastern Pacific. The new species is hereby described and illustrated, contributing to the species and genetic biodiversity of the munidid fauna in the eastern Pacific.

Materials and methods

Sample collection and morphological examination

The material for this study was collected during the Schmidt Ocean Institute research cruise FK190106 in the seamount area of Cocos Canyon, off the Pacific coast of Costa Rica. The specimen was collected using the remotely operated vehicle (ROV) *SuBastian* deployed from the research vessel *Falkor*. The collected specimen was photographed alive and fixed in 95% ethanol. Specimen collection and field operations in Costa Rica were performed under permits INCOPESCA-CPI-003-12-2018 and R-070-2018-OT-CONAGEBIO, issued by the Government of Costa Rica. DNA sequencing for this project was authorized by the contract for the grant of prior informed consent between MINAE-SINAC-ACMC

and Jorge Cortés Núñez for the basic research project: “FK190106 – Cuantificación de los vínculos biológicos, químicos y físicos entre las comunidades quimiosintéticas con el mar profundo circundante.”

The size of the specimen is given as the postorbital carapace length (pcl), which refers to the carapace length excluding the rostrum. The terminology used mainly follows Machordom et al. (2022). The specimen collected during the expedition was deposited in El Museo de Zoología de la Universidad de Costa Rica (MZUCR), and a tissue sample was deposited in the Scripps Institution of Oceanography Benthic Invertebrate Collection (SIO-BIC). The abbreviations used in the text are as follows: P1, pereiopod 1 (chelipeds); P2–4, pereiopods 2 to 4 (first to third walking legs).

DNA extraction, amplification, and sequencing

To explore the relationships of the new species with other munidid species from the eastern Pacific, we included *T. propinqua* and *A. bapensis*, which are deposited at SIO-BIC, and the holotype of *T. alba* (with the help of Dr. Liu Xinming, currently deposited at the Marine Biology Museum, Chinese Academy of Sciences), in the phylogenetic study (Suppl. material 1). These three species, together with the new species, were selected for gene marker sequencing in this study.

Total genomic DNA was extracted from pereiopods and abdominal muscle tissue using the Zymo Research DNA-Tissue Miniprep Kit (Irvine, California, USA) and EasyPure Marine Animal Genomic DNA Kit (TransGen). Partial sequences of two mitochondrial genes, cytochrome c oxidase subunit I (COI) and 16S rRNA (16S), and one nuclear gene, histone 3 (H3), were amplified via polymerase chain reaction (PCR). The primers used for COI amplification were HCO2198 and LCO1490 (Folmer et al. 1994). The primers used for 16S amplification were 16Sar and 16S1472 (Simon et al. 1994; Crandall and Fitzpatrick 1996). The primers used for H3 amplification were AF and AR (Colgan et al. 1998). Reactions were carried out following the original procedures with minor modifications. PCR products were purified using the ExoSAP-IT protocol (USB Affymetrix, Ohio, USA), and Sanger sequencing was performed in both directions by Eurofins Genomics (Louisville, Kentucky, USA) and Tsingke Biotech Co., Ltd. (Beijing, China). Sequences were checked and assembled based on the contigs using the DNASTAR LASERGENE software package (DNASTAR, Inc., Madison, WI, USA). New sequences obtained in this study were deposited in GenBank (PQ599895–PQ599898, PQ604650–PQ604652, PQ621049–PQ621051).

Genetic distances and phylogenetic analyses

A total of 124 sequences (including three genes) of 46 species in Munididae were downloaded from NCBI GenBank for genetic distances and phylogenetic analyses

(Suppl. material 1). These species cover all 11 genera newly established or revised by Machordom et al. (2022) from *Munida sensu lato*, and another two genera, *Babamunida* Cabezas, Macpherson & Machordom, 2008, and *Garymunida* Macpherson & Baba in Machordom et al. 2022, to represent all four major lineages of Munididae recovered in Machordom et al. (2022). To verify the systematic status of the new species, we included all the available genetic data for the genus *Typhlonida* (species with at least a COI sequence), as well as all species of Munididae from the eastern Pacific in the phylogenetic study (Suppl. material 1). *Munidopsis kexueae* Dong, Gan & Li, 2021 was chosen as the outgroup.

The sequences of each gene were aligned using the software MAFFT (Kato and Standley 2013) and then manually trimmed. The average genetic distances between the new species and closely related species, based on COI sequences, were estimated under the Kimura 2-parameter model (Kimura 1980) in MEGA 6 (Tamura et al. 2013).

The two mitochondrial genes were combined to generate a “mito-dataset,” which includes 51 species (including the new species and outgroup, similarly hereinafter). All three genes were concatenated to generate an “all-dataset” (including 39 species with the H3 gene and at least one mitochondrial gene). Both datasets were partitioned by genes and codons, and the best nucleotide base substitution models were estimated using PARTITIONFINDER 2 (Lanfear et al. 2017). Phylogenetic relationships were inferred from both datasets using maximum likelihood (ML) by IQ-TREE (Nguyen et al. 2015) and Bayesian inference by MRBAYES (Ronquist et al. 2012). Nodal supports of ML trees were evaluated in two approaches: SH-aLRT branch test (Guindon et al. 2010) using 1000 replicates and ultrafast bootstrap (UFBoot) with 5000 replicates (Minh et al. 2013). Bayesian inferences were

run for at least 3 million generations, and the nodal support was assessed with posterior probabilities (PP). The first 25% of the initial trees were discarded as burn-in. The implementation of MAFFT, PARTITIONFINDER2, IQ-TREE, and MRBAYES was pipelined in the program PHYLOSUITE (Zhang et al. 2020).

Result

Phylogenetics

Ten new sequences were obtained in this study: four of COI, three of 16S, and three of H3. The final alignment length of each gene was as follows: COI (639 bp), 16S (506 bp), and H3 (328 bp).

The phylogenetic trees generated from the mito-dataset (Fig. 1) and all-dataset (Suppl. material 2) were mostly congruent. Similarly, the topologies of the ML and Bayesian trees were consistent on the relationships of the main clades. According to the trees derived from the mito-dataset, the new species was paired with *T. sanctipauli* (Henderson, 1885), but this relationship was only supported by the UFBoot value (= 100). All the species of *Typhlonida* formed a clade, which roughly contained two subclades. One subclade (subclade I) included only species from the eastern Pacific and Atlantic Oceans, with high support in the mito-dataset trees (SH-aLRT = 89.4, PP = 0.99), while in the all-dataset-derived trees, it was only supported by the PP value (=0.99). It is noteworthy that *Antillimunida bapensis* was recovered within this subclade, rather than clustering with other *Antillimunida* species. A second subclade (subclade II), which mainly consists of Indo-West Pacific species, was highly supported by all inference methods.

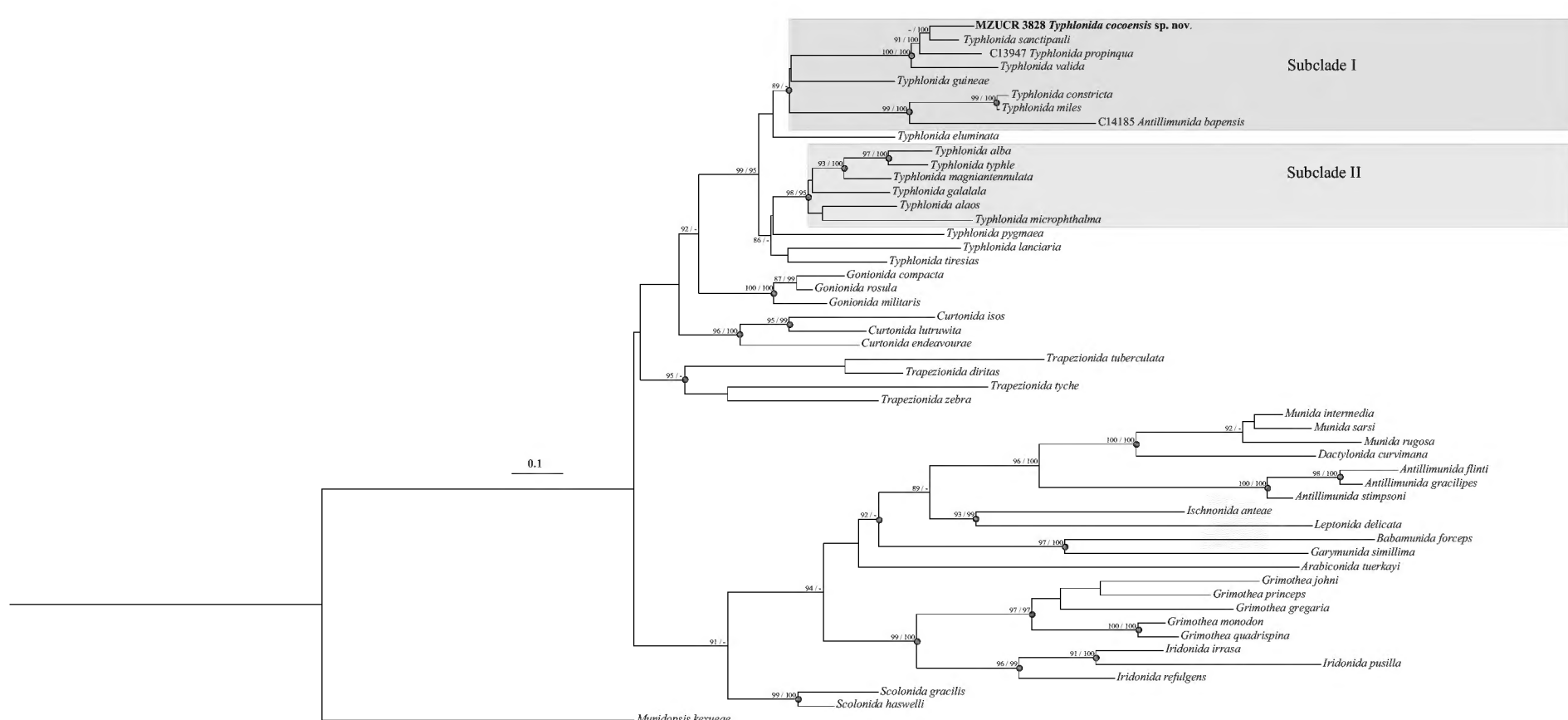


Figure 1. Phylogenetic tree obtained after the maximum likelihood analysis based on the mito-dataset. SH-aLRT value (percentage, left) and UFBoot value (right) are indicated adjacent to each node. Only values of SH-aLRT $\geq 85\%$ and UFBoot $\geq 95\%$ are shown. Nodes with PP support above 0.95 are marked with red circles.

Systematics

Superfamily Galatheoidea Samouelle, 1819

Family Munididae Ah Yong, Baba, Macpherson & Poore, 2010

Genus *Typhlonida* Macpherson & Baba in Machor-dom et al., 2022

Typhlonida cocoensis sp. nov.

<https://zoobank.org/6D7B968B-78B4-4FD8-B5CB-FA58E9B00AFB>

Figs 2–5

Material examined. *Holotype* • MZUCR 3828 (tissue sample SIO-BIC C13940), female (pcl 10.7 mm), Cocos Canyon, Isla del Coco, Costa Rica, eastern Pacific, 5.5821°N, 87.0657°W, 831.5 m, coll. Greg Rouse and Avery Hiley, using ROV *SuBastian* on R/V *Falkor*, dive S0223, event S8, cruise FK190106, 18 January 2019.

Diagnosis. Carapace slightly longer than broad (excluding rostrum); branchial margins with 5 spines; posterior margin unarmed. Sternite 3 posterior margin contacting sternite 4 on median 0.3 part; sternite 4 triangular; lateral surfaces of sternite 7 smooth. Pleonal tergites 2 with 9 spines on anterior ridge. Eyes moderately large; diameter of cornea approximately twice wider than sinus between rostral spine and supraocular spine. Basal article of antennular peduncle with distolateral spine more than twice longer than distomesial spine. Merus of third maxilliped with three spines on flexor margin. Lateral margin of P1 fixed finger with small paired subterminal spines followed by row of spines; mesial margin of P1 dactylus only with basal spine.

Description. Carapace: Slightly longer than broad (excluding rostrum), approximately 1.3 times longer than broad. Frontal margin oblique. Lateral margins slightly convergent posteriorly; anterolateral spines strong, tip falling short of base of supraocular spine; hepatic margin convex, with acute spine and additional small spines; branchial margin armed with 5 spines; posterior branchial margin with oblique ridges; posterior margin unarmed. Dorsal surface gently convex transversely; cervical grooves clear; main transverse ridges present on gastric, cardiac, intestinal, and posterior branchial regions bearing fine setae anteriorly; short scale-like rugae present among main ridges and on epigastric, hepatic, and anterior branchial regions; postcervical spines well developed; gastric region elevated, with pairs of strong epigastric spines posterior to supraorbital spines and each flanked by relatively short mesial and posterolateral spines; additional pair of minute epigastric spines present laterally. Rostral spine spiniform, dorsally carinate, approximately 0.4 times remaining carapace length, horizontal in lateral view; supraocular spines spiniform and subparallel, smoothly carinate, approximately 0.4 times of rostral spine length, slightly overreaching distal end of cornea. Pterygostomial flaps with transverse or oblique ridges on lateral surface, anterior part with shallow groove near dorsal margin; anterior end with acute small spine.

Sternal plastron: longer than broad; posterior margin distinctly concave. Sternite 3 approximately 3.6 times as broad as long, anterior margin bilobate and faintly denticulate; posterior margin contacting sternite 4 on median 0.3 part; lateral parts slightly bent ventrally. Sternite 4 triangular, anterolateral margins straight; ventral surface excavated, bearing several scale-like rugae. Sternite 5 and 6 with transverse, interrupted ridges and shallowly grooved along midline. Sternite 7 smooth on lateral parts, with oblique ridges posteriorly and deep cavity medially.

Pleon: Tergite 2 with 9 spines evenly along anterior ridge. Dorsal surfaces of tergites 2–5 each with 2 transverse ridges interspaced by shallow groove; lateral part of each segment with scale-like rugae.

Telson: Broader than long; divided into 8 plates. Dorsal surface with scale-like rugae.

Eyes: Moderately large. Cornea dilated, hemispheric, slightly wider than eyestalk, diameter approximately twice wider than sinus between rostral spine and supraocular spine, and third of distance between bases of anterolateral spines. Distal margin of cornea reaching proximal third of rostral spine; eyelash dense.

Antennular peduncle: Basal article (excluding distal spines) approximately 2.3 times longer than broad, reaching distal 0.4 of rostral spine. Distolateral spine more than twice longer than distomesial spine. Lateral margin with 2 median spines. Ventral surface with scale-like rugae.

Antennal peduncle: Reaching distal cornea margin. Article 1 immovable, with strong distomesial spine hardly reaching distal end of article 2. Article 2 armed with strong distomesial spine reaching distal end of article 3, and distolateral spine falling short of distal end of article 3; mesial margins with small median tubercles. Article 3 subrectangular, unarmed. Article 4 short and unarmed.

Third maxilliped: Ischium slightly longer than merus, with weak distoflexor and disto-extensor spines; ventral surface with row of short rugae on midline. Merus with three spines on flexor margin: proximal and distal spines strong, median spine minute; extensor margin strongly rugose, with small distal spine; ventral surface scattered with short rugae. Carpus, propodus, and dactylus unarmed.

P1: Subequal, 1.8 times pcl; each segment covered with thick, long, and non-iridescent setae, bearing numerous scale-like rugae on surfaces and margins. Merus approximately 0.7 times PCL, 3.9 times as long as broad; distal margin with strong dorsal, dorsomesial, ventromesial, and lateral spines; distal dorsal spine followed by row of 7 spines or acute tubercles decreasing in size proximally extending to proximal end of merus; distal dorsomesial spine followed by 2 dorsal spines and another prominent ventral spine. Carpus subcylindrical, approximately half of merus length, 2.0 times longer than broad; distal margin with distinct dorsal, dorsomesial, and small ventrolateral spines; distal dorsal spine followed by row of 4 spines on dorsal midline, distal dorsomesial spine followed by row of 4 spines (distal second and third spines most prominent), 2 spines along dorsolateral margin, 2 spines on ventral midline, several tubercle-like spines on lateral margin,

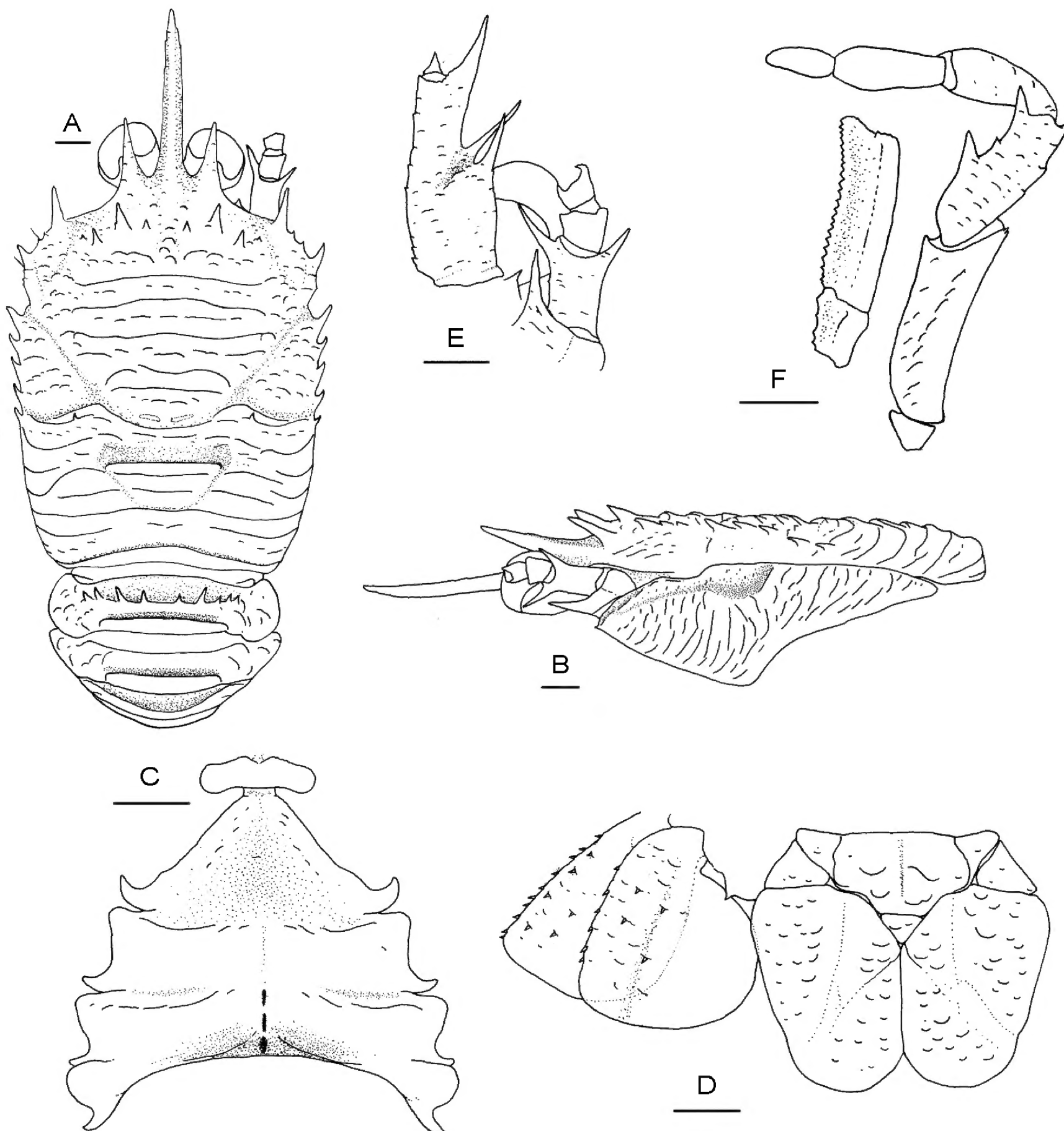


Figure 2. *Typhlonida cocoensis* sp. nov., MZUCR 3828, holotype, female. **A.** Carapace and pleonal tergite 1–4, dorsal view; **B.** Carapace and left pterygostomian flap, lateral view; **C.** Sternal plastron, ventral view; **D.** Telson and left uropod; **E.** Left antennular and antennal peduncles, ventral view; **F.** Left third maxilliped, ventral view. Scale bars: equal 1.0 mm.

and 2 or 3 small spines near distoventral margin. Palm relatively compressed, 0.6 times merus length, 2.7 times longer than broad; dorsal surface with small distal spine adjacent to base of dactylus and row of 3 spines along mid-line, dorsomesial margin with row of 5 spines, dorsolateral margin with row of 17 spines of different sizes extending from proximal end of palm to subdistal end of fixed finger, ventromesial margin with row of 5 spines (distalmost spines much prominent). Fingers approximately 0.9 times palm length, tips hooked; occlusal margins nearly straight, denticulate; lateral margin of fixed finger with small paired subterminal spines followed by row of spines mentioned above; mesial margin of movable finger with single strong basal spine and acute tubercles proximally.

P2 and P4 (P3 missing): Surfaces of merus, carpus, and propodus with fine rugae; extensor margins bearing dense setae; P2 approximately 1.6 times pcl, reaching midlength of P1 palm. Meri compressed; P2 merus approximately 0.6 times pcl, P4 merus 0.7 times P2 merus length; length-width ratio: P2 and P4 meri being 5.2 and 4.3, respectively; extensor margin with row of slender spines (disto-extensor spine strongest) on P2, and scattered minute spines on P4; flexor margin with row of spines (decreasing in size proximally) on entire length of P2, and only single strong distal spine followed by row of elevated scale-like rugae on P4. Carpi subequal in length and width on P2 and P4, approximately 0.3 times P2 merus length; extensor margin with 2 longitudinal ridges, mesial ridge with 4 spines

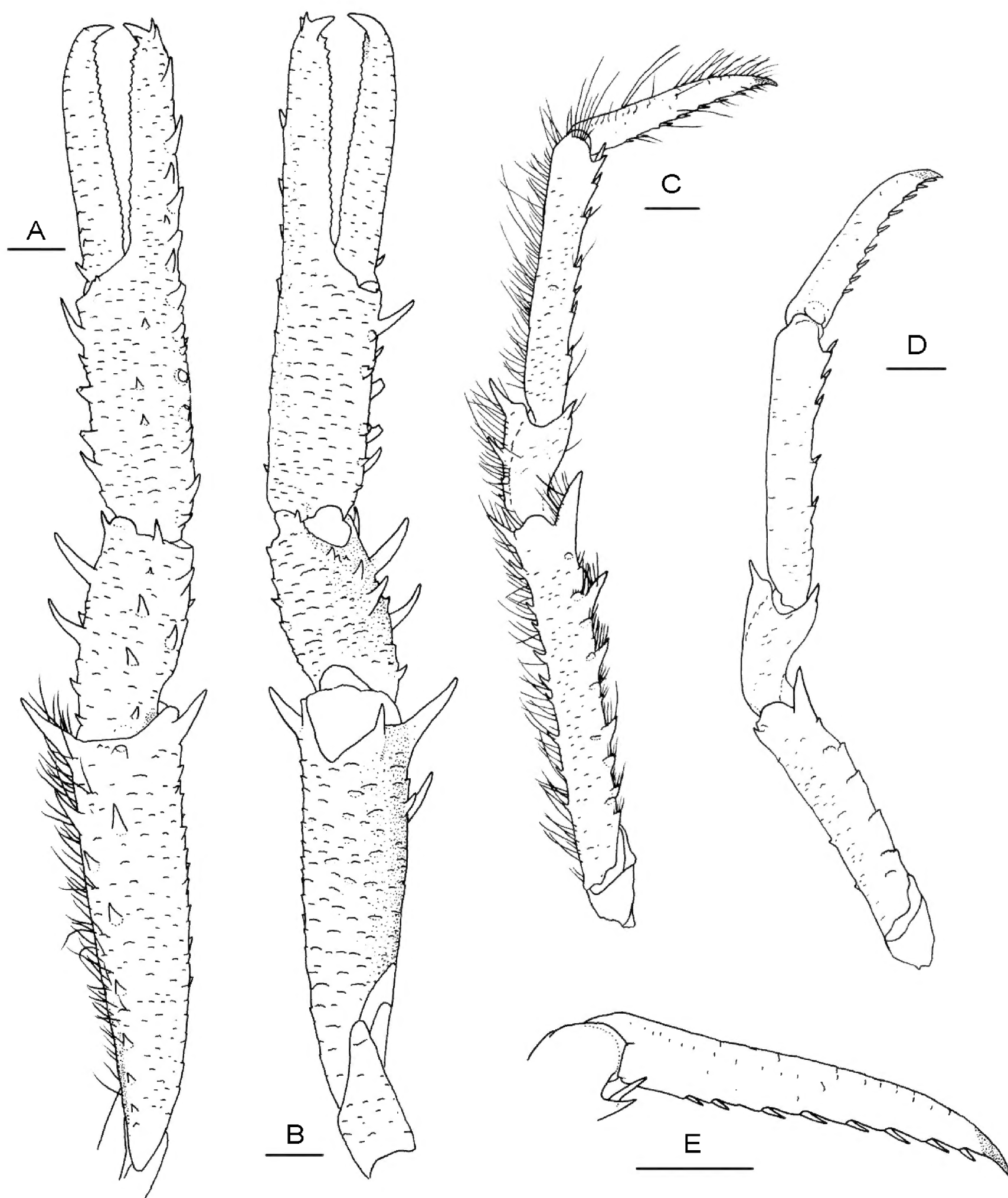


Figure 3. *Typhlonida cocoensis* sp. nov., MZUCR 3828, holotype, female. **A.** Right P1, setae illustrated only on mesial margin of merus, dorsal view; **B.** Right P1, ventral view; **C.** Right P2, lateral view; **D.** Right P4, lateral view; **E.** Dactylus of right P2, lateral view. Setae omitted on **B**, **D**, and **E**. Scale bars: equal 1.0 mm.

(distal two much prominent) on P2 and only single distal spine on P4, lateral ridge low and unarmed; flexor margin with prominent distoflexor spine. Propodi slender, subequal in width; P4 propodus 0.9 times P2 propodus length; length-width ratio: P2 and P4 propodus being 7.2 and 6.3, respectively; extensor margin straight; flexor margin with 5–7 corneous spines, distalmost spine based on acute tooth paired with small mesial spine. Dactyli subequal in length, P2 dactylus approximately 0.6 times of P2 propodus length, 5.7 times longer than broad; extensor margin

straight, with feeble rugae; flexor margin straight, armed with 8 or 9 movable corneous spines on entire length.

Coloration. Dorsal surfaces of carapace and pleon generally light orange; anterior part of carapace, including rostral spine, supraocular spines, anterolateral spines, and epigastric spines, red-orange. Pereiopods whitish.

Habitat. Submarine canyon on the flank of Isla del Coco, Costa Rica.

Distribution. Only known from the type locality, depth 831.5 m.

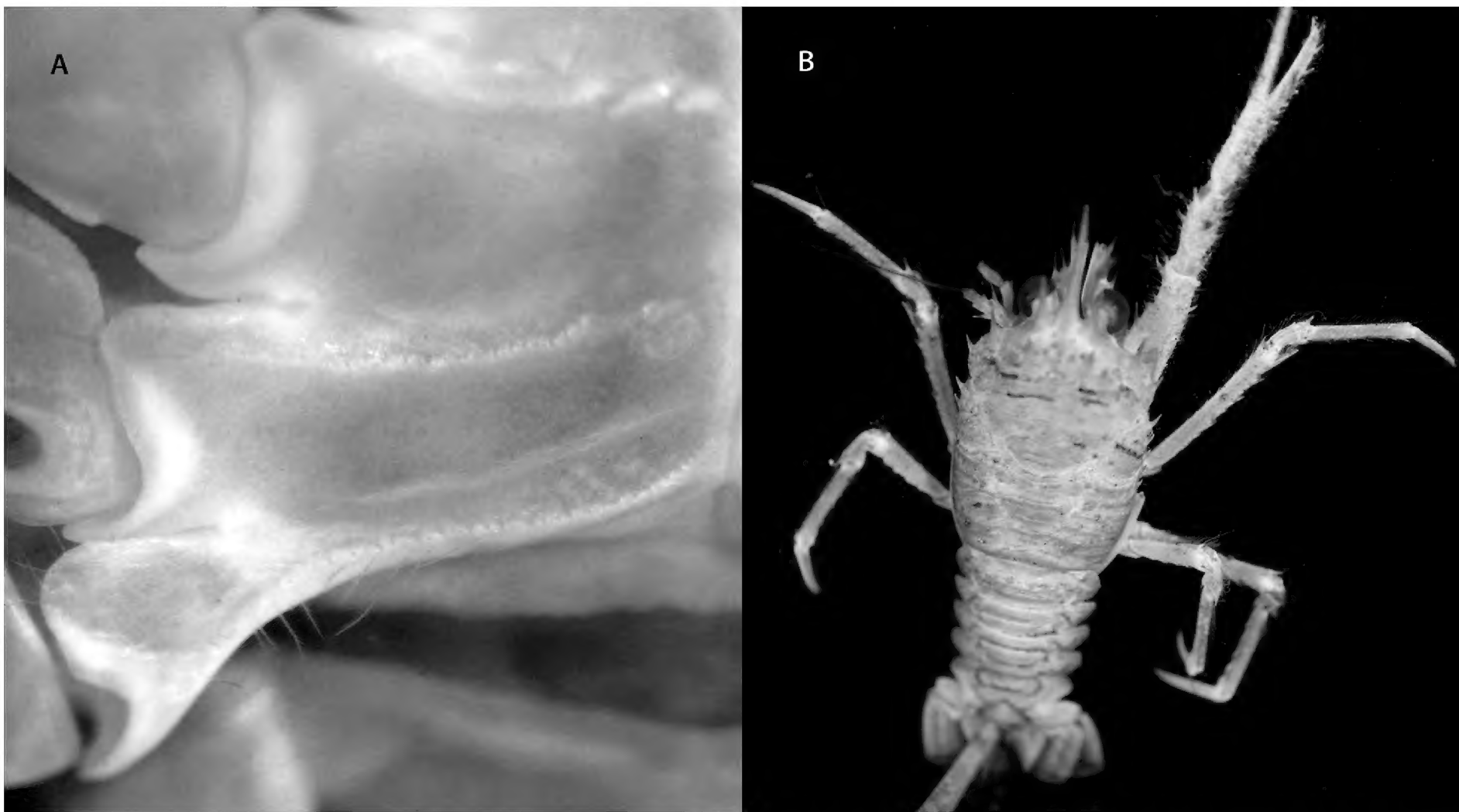


Figure 4. *Typhlonida cocoensis* sp. nov., MZUCR 3828, holotype, female. **A.** Sternite 5–7 on the right side, ventral view; **B.** color in life, dorsal view.

Etymology. Named in honor of the type locality off Isla del Coco (Cocos Island), an oceanic island protected within Parque Nacional Isla del Coco and designated as a UNESCO World Heritage Site for its rich biodiversity. We thank Jorge Cortés Núñez, Universidad de Costa Rica, for proposing this name and for his contributions to deep-sea research and biodiversity studies of Isla del Coco (Cortés 2012).

Remarks. The new species is characterized by the moderately dilated cornea, distomesial spine of antennular article 1 less than half length of distolateral spine, short distomesial spines of basal and second antennal articles, 5 branchial marginal spines, and triangular and narrow thoracic sternite 4. These morphological features link the new species to the genus *Typhlonida* (Machordom et al. 2022). The new species has flat and smooth lateral surfaces of the thoracic sternite 7, with the transverse ridges of sternite 7 extending posterior to rather than onto the lateral surface. This character distinguishes the new species from other congeners in *Typhlonida*. This character assimilates the new species to a group of species with lateral surfaces of sternite 7 granulated. For the new species, however, no granulation was observed on the lateral surfaces (Fig. 4A).

The new species is morphologically close to *T. sanctipauli*, which is distributed in the East and West Atlantic Ocean (Baba et al. 2008). Both species have a row of spines only on the anterior ridge of pleonal tergite 2, 2 flexor spines on the merus of the third maxilliped, and the P2 meri with row of spines on the flexor margin. The new species differs from *T. sanctipauli* in the following characters: The eyes are relatively small with the cornea width approximately a third of the distance between bas-

es of the anterolateral spines; anterior margin of the thoracic sternite 4 is very narrow, contacting median 0.3 of the posterior margin of sternite 3; the lateral surfaces of sternite 7 are smooth; and the anterior branchial regions are unarmed. In *T. sanctipauli*, the eyes are comparatively large with the cornea width more than 0.4 times the distance between the bases of the anterolateral spines; anterior margin of the sternite 4 broad, contacting at least half length of the posterior margin of sternite 3; the lateral surfaces of sternite 7 are granulated; and the anterior branchial region has one dorsal spine (de Saint Laurent and Macpherson 1988; de Melo-Filho and de Melo 1992).

Among the munidid species distributed in the eastern Pacific, the new species is morphologically similar to *Grimothea curvipes*, which is known only from the deep sea (1890–2743 m) off southern Chile (Retamal et al. 2020). Both species have five branchial marginal spines, a moderately dilated cornea, a narrow anterior margin of sternite 4, a row of spines on the anterior ridge of pleonal tergite 2, two flexor spines on the merus of the third maxilliped, and a row of spines on the flexor margin of P2 meri. The genus *Grimothea* Leach, 1820, is characterized by article 1 of the antennal peduncle being fused with the lateral margin of the epistome. By contrast, *Typhlonida* and other munidid genera (except *Iridonida*) have this article clearly separated from the epistome. This feature, however, is still unclear on *G. curvipes* based on the previous descriptions of the holotype (Benedict 1902; Hendrickx 2003); therefore, the taxonomic position of *G. curvipes* remained dubious and temporarily assigned to *Grimothea* (Machordom et al. 2022). Besides the difference in generic characters, the new species readily differs from *G. curvipes* in having

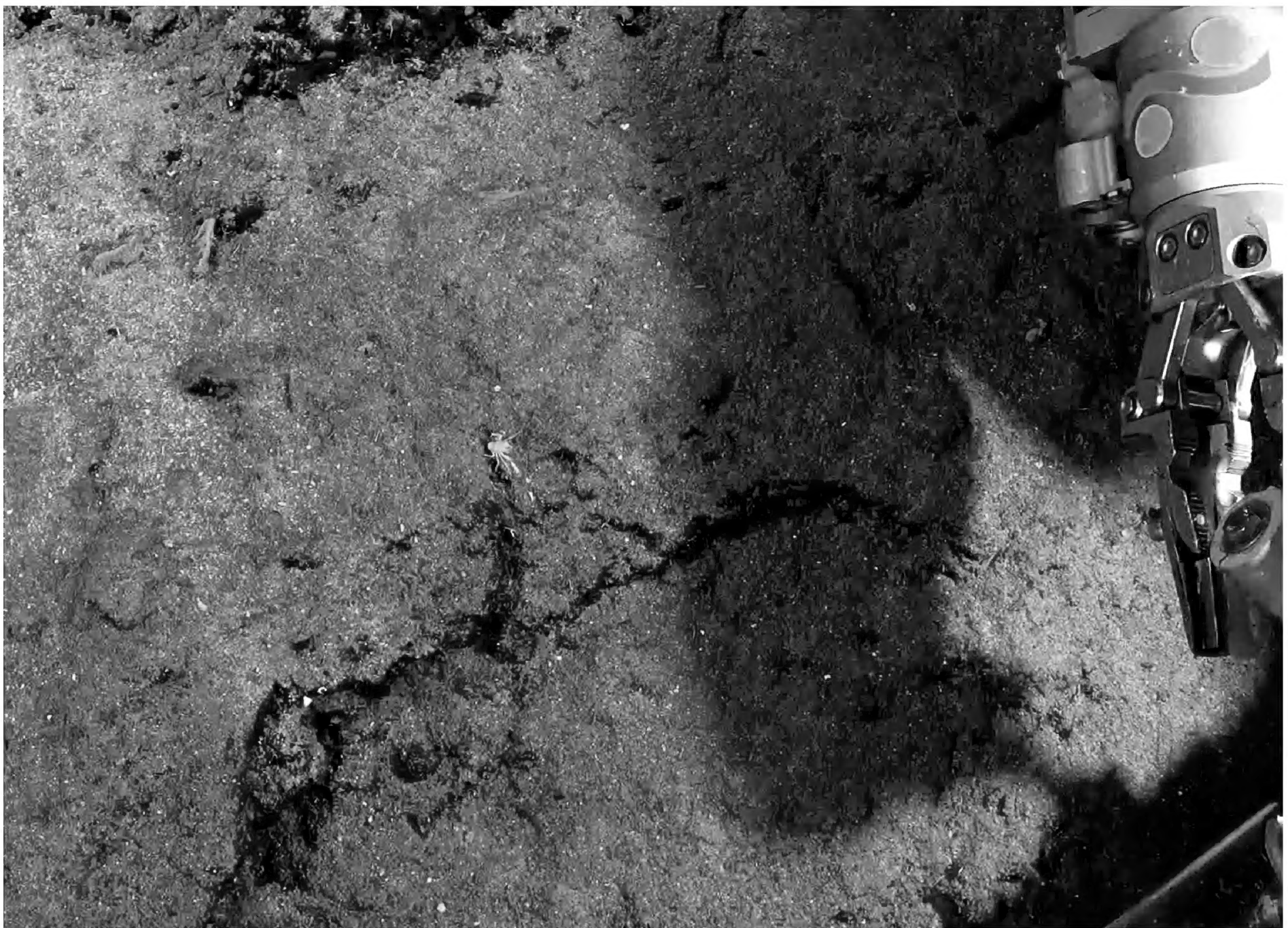


Figure 5. *Typhlonida cocoensis* sp. nov. in habitat; depth 831.5 m, Cocos Canyon; image credit ROV SuBastian/Schmidt Ocean Institute.

flat and smooth lateral surfaces of sternite 7, a short distomesial spine of antennular article 1, unarmed articles 3 and 4 of the antennal peduncle, a weak distoflexor spine of the third maxilliped ischium, and a row of spines on the entire lateral margin of the P1 fixed finger. In *G. curvipes*, the transverse ridges of sternite 7 extend onto the lateral surfaces; the distomesial and distolateral spines of antennular article 1 are subequal (distolateral spine slightly longer); articles 3 and 4 of the antennal peduncle each have small distolateral spines; the ischium of the third maxilliped has a strong distoflexor spine; and the P1 fixed finger only has distal and basal spines (Hendrickx 2003).

Only three *Typhlonida* species have been previously reported in the eastern Pacific: *T. alba*, *T. perlata*, and *T. propinqua*. Due to the lack of molecular data, all these species were assigned to *Typhlonida* based on morphology (Machordom et al. 2022). The new species resembles *T. perlata*, which occurs in the deep sea from the Gulf of California to the Galápagos Islands (Baba et al. 2008). Besides the structure of the sternite 7, *T. perlata* is different from the new species in having a relatively small cornea of the eyes with the diameter approximately as wide as the sinus between the rostral spine and supraocular spine (instead of more than two times wider), the flexor margin of the third maxilliped merus with a single spine (instead of two spines), and the dactylus of the P1 unarmed on the mesial margin (instead of with a strong basal spine) (Hendrickx 2000).

Faxon (1893, 1895) once reported *Munida microphthalma* (= *T. microphthalma*) from Cocos Island based on a single ovigerous female, but the identity of the specimen was in doubt (Hendrickx 2000; Baba et al. 2008). *Typhlonida microphthalma* differs from the new species in having the granulated lateral surfaces of sternite 7, the much-reduced cornea, and the antennal article 3 armed with a distomesial spine (Hendrickx 2000). Faxon (1893, 1895) noted that the Cocos specimen had no spines on the P1 dactylus and the dorsal surface of the palm, and only two spines on the pleonal tergite 2; these characters are also inconsistent with those of the new species.

The smallest genetic distance based on COI was observed between the new species and *T. sanctipauli*, at 5.8%, showing a moderate genetic divergence commensurate with other interspecific distances in Munididae (Macpherson et al. 2024). The GenBank accession numbers of sequences obtained in this study are provided in Suppl. material 1.

Discussion

The phylogenetic trees recovered in this study are congruent with those of Machordom et al. (2022) regarding the monophyly of each genus. The *Typhlonida* clade can essentially be divided into two subclades, which is also

consistent with the results of Machordom et al. (2022), based on the concatenated genes and COI sequence, respectively (figs 7 and S2 in Machordom et al. 2022).

The new species, together with *T. propinqua* and *T. alba*, was placed within the *Typhlonida* clade in both trees derived from the mito-dataset (Fig. 1) and all-dataset (Suppl. material 2). The new species was sister to *T. sanctipauli*, supported by a robust ultrafast bootstrap value (from the mito-dataset), demonstrating an agreement of the phylogenetic and morphological analyses on the relationship between the two species. In subclade I, the new species and two other eastern Pacific species (*T. propinqua* and *A. bapensis*) were grouped with five species from the Atlantic Ocean. *Typhlonida* is characterized by having small corneas (Machordom et al. 2022). However, these eight species have relatively large or moderate-sized eyes with the cornea markedly dilated, resulting in the projection of the supraocular spine on the median or mesial part of the cornea. In contrast, *Typhlonida* species in subclade II have much-reduced small corneas, with most parts of the eye-stalk and cornea located between the supraocular spine and the rostral spine. It is interesting to note that subclade II includes species from the West Pacific, eastern Pacific, and Atlantic Oceans, suggesting that the members of this phenotype are globally distributed. The phylogenetic status of other *Typhlonida* species, however, remains still unclear, as they do not belong to any subclade with significant support according to the results of both ML and BI analyses.

It is noteworthy that *A. bapensis* was within the *Typhlonida* clade, which was supported by each inference method. Molecular data of the *Antillimunida* species from the eastern Pacific were lacking in previous studies. *Antillimunida* morphologically differs from *Typhlonida* mainly in having a spinose posterior margin of the carapace, a longer P4 merus distally reaching to the anterior margin of the carapace, and a single spine on the flexor margin of the third maxilliped merus (Machordom et al. 2022). Re-examination of the specimens of *A. bapensis* and *A. hispida* from SIO-BIC shows that both species have a short P4 merus and at least two flexor spines on the third maxilliped merus. However, the spine patterns on the carapace can still link the two species to other congeners.

Machordom et al. (2022) inferred that the ancestral range for most of the munidid lineages was in the West Pacific region; nevertheless, for *Typhlonida*, the eastern Pacific specimens were absent in that biogeographic analysis. It is necessary to include more species and sufficient genetic data, particularly from type localities, in the future to clarify the true systematic status of the two genera *Typhlonida* and *Antillimunida*, as well as their evolutionary history and dispersal route around the world.

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Supplementary material 1

Species and GenBank accession numbers of sequences included in present study

Authors: Dong Dong, Charlotte A. Seid, Xinzheng Li, Greg W. Rouse

Data type: docx

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Supplementary material 2

Phylogenetic tree obtained by the maximum likelihood analysis based on the all-dataset

Authors: Dong Dong, Charlotte A. Seid, Xinzheng Li, Greg W. Rouse

Data type: pdf

Explanation note: SH-aLRT value (percentage, left) and UFBoot value (right) are indicated adjacent to each node. Only values of SH-aLRT $\geq 85\%$ and UFBoot $\geq 95\%$ are shown. Nodes with PP support above 0.95 are marked with red circles.

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